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THE EFFECT OF THE SUBANTARCTIC ENVIRONMENT ON ASPECTS OF THE TERRESTRIAL PHASE OF FUR SEAL POPULATIONS

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Résumé

Les pinnipèdes sont incapables de thermoréguler efficacement par les seuls moyens physiologiques quand ils sont à terre, car leurs adaptations sont d'abord aquatiques. Les otaries se réunissent pour se reproduire sur les îles subantarctiques au cours de l'été austral. Elles utilisent des ajustements comportementaux pour faire face à l'augmentation de la température interne durant la phase terrestre de leur cycle saisonnier. Ceci s'exprime par leur choix d'habitat particulier et leur distribution locale, et peut varier avec la topographie des plages disponibles ainsi que la position des îles en rapport avec la convergence antarctique. Nous comparons deux espèces d'otaries *Arctocephalus tropicalis,* l'otarie d'Amsterdam et *A. gazella,* l'otarie de Kerguelen, qui occupe des îles de haute et basse latitudes où différents paramètres physiques du milieu terrestre agissent.

Les caractéristiques de l'otarie et du milieu sont données et les interactions décrites en liaison avec des aspects choisis.

Abstract

Pinnipeds are unable to thermoregulate effectively by physiological means alone when on land since their primary adaptations are aquatic. Fur seals congregating on sub-Antarctic islands during the austral summer breeding season make use of behavioural adjustments to cope with excessive exogenous heat input during the terrestrial phase of their seasonal cycle. This finds expression in their particular habitat selection and local distribution, and may vary with the topography of the available beaches, and the position of the islands in relation to the Antarctic Convergence. Two fur seal species, the Subantarctic fur seal *Arctocephalus tropicalis* and the Antarctic fur seal *A. gazella,* which occur on high and low latitude islands where concomitant different terrestrial physical environmental factors are in operation, are discussed. Characteristics of both the seal and the environment are given, and the interaction described with reference to selected aspects.

INTRODUCTION

The most outstanding feature of pinnipeds is the unique combination of terrestrial parturition and offshore marine feeding. Clearly the invasion of the marine environment has been accompanied by morphological and physiological adaptations in the course of evolution, which furthermore has led to constraints on the seals during their terrestrial phase. Gregariousness and polygyny occur in all pinniped species breeding on sub-Antarctic islands. This allows these animals, which are highly dispersed during the nonbreeding season, to congregate and breed on these oceanic inlands during the austral spring and summer, despite the fact that

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their primary adaptations are aquatic. The present paper deals with the influence of the insular terrestri environment on fur seal populations in particular, although the influence of the availability, distributi and abundance of marine food resources may contribute to the observed effects. Two fur seal species, t Antarctic fur seal *Arctocephalus gazella,* and the Subantarctic fur seal *A. tropicalis* are primarily referr to since their breeding localities range from 37 °S to 62 °S, *A. gazella* generally occurring to the sou of the Antarctic convergence, and *A. tropicalis* to the north of it. Concomitant differences in terrestri environmental factors are therefore in operation. Characteristics of both seal and environment are give and the interaction between them is described with reference to selected aspects.

THE FUR SEAL

Pinnipeds are adapted to conserve heat in their normally cold marine surroundings. The heat retaini devices of fur seals, a layer of subcutaneous blubber of varying thickness, and a pelage consisting of gua hairs and underfur fibres of varying density and composition, restrict heat loss in sea water with its hi thermal capacity. Even in cold water, body temperature extends to the skin in the northern fur seal *Callorhin ursinus,* and the important insulation is provided by the waterproof fur (Irving, Peyton, Bahn & Peterso 1962).

The naked flippers are the major site for heat dissipation (McGinnes, Cryer & Hubbard, 197 Whittow, Matsuura & Lin, 1970) and rapid lowering of the temperature of the hind flippers of f seals are a means to conserve body heat (Irving *et al.,* 1962). On land, however, the constant insulati provided by the pelage poses a thermoregulatory problem to fur seals under the higher range of ambie temperatures and solar radiation encountered.

Physiological means of body temperature regulation open to pinnipeds are heat dissipation by vasomot regulation of heat flux across the skin, cutaneous evaporation, heat storage, nonevaporite heat loss to air the form of heat conduction and radiation, and respiratory evaporative cooling. It has been shown that the are, however, unable to regulate their body temperature effectively on land by physiological means alone durin thermal loading. Behavioural adaptations are required to supplement physiological thermoregulation in t otariidae, for example, sandflipping (Vaz-Ferreira, 1975) flipper waving (Bartholomew & Wilke, 195 Peterson & Bartholomew, 1967 ; Rand, 1967), postural adjustments related to the degree of exposure the flippers (Bonner, 1968 ; Gentry, 1973 ; Bester, 1977), use of shade (Orr, 1967 ; Peterson, Hubb Gentry & De Long, 1968 ; Gentry, 1973), urohidrosis (Gentry, 1973 ; Whittow, Matsuura & Ohat 1975), panting and open-mouth type of breathing (Bartholomew & Wilke, 1956 ; Rand, 1967 ; Whitto *et al.,* 1975) or resorting to water and/or wet sand (Rand, 1967 ; Stirling, 1970 ; Gentry, 1973 ; Mille 1974 ; Vaz-Ferreira, 1975).

Most of these behavioural responses to high ambient temperatures have been described for the *Arct cephalus* genus as a whole (Bester, 1977) and it can be accepted that physiologically, mechanisms f thermoregulation are the same for all its members. Furthermore, until recently accorded subspecific stat following King (1959), they are at present apparently interbreeding under natural conditions at Marion Isla (Condy, 1978). The different responses to the demands of their terrestrial environment and climatic factors *A. gazella* and *A. tropicalis* therefore seem unlikely to be ascribed to inherent morphological and physiologic differences, but solely to the environmental factors in operation.

THE INSULAR TERRESTRIAL ENVIRONMENT

Sub-Antarctic islands all lie in the cold waters of the West Wind Drift (Taljaard, 1957), with expose westerly coastlines and more protected leeward east coast beaches. From low (northerly) to high (southerl latitudes, in that order, *A. tropicalis* breed on the Tristan da Cunha Island group (± 37° S, 12° E), Amsterda

TABLE I

Climatic data from low, mid and high latitude Islands for the period November-January mean air temperatures in °C, relative humidity in %, and cloud coverage in octas.

	Gough* Island	Marion** Island	Bird*** Island
Mean air temp. (T_m)	12,7	5,9	2,5
Mean max. temp. (T_x)	15,5	15,5	3,7
Mean min. temp. (T_n)	9,8	– 0,1	1,5
Mean abs. max. (T_{xx})	21,6	20,6	6,3
Mean abs. min. (T_{nn})	5,4	– 0,8	– 1,0
Mean relative humidity (U)	83	81	91
Mean cloud coverage (N)	6,4	6,3	7,6

* Data for 1966-1970 from the *Report on Meteorological Data,* South African Weather Bureau, Department of Transport

** Data for 1961-1965, Schulze (1971)

*** Data from 1958 and 1959, Bonner 1968.

and Saint Paul Islands (± 38° S, 77° E), Gough (± 40° S, 10° W), MARION and Prince EDWARD (46° S, 38° E) Islands, as well as the Crozet group (46° S, 51° E). *A. gazella* also occur at MARION and Prince EDWARD Islands, but mainly further south at for example Kerguelen (49° S, 73° E), Bouvet (54° S, 3° E), the South Sandwich (54° S, 26° W), South Orkney (60° S, 45° W) and South Shetland Islands (62° S, 60° W), and principally at South Georgia (55° S, 37° W).

Climatic data from representative low, mid and high latitude islands are shown in Table I. The climates re characterized by their extreme oceanicity. Westerly winds predominate and in summer, from November o January during the fur seal pupping season, "high" ambient air temperatures may prevail. Low latitude slands experience significantly higher ambient air temperatures, especially mean maximum temperatures, while ittle variation in mean cloud coverage and mean relative humidity are evident. Furthermore, leeward east oast beaches generally seem to experience warmer and clearer weather, when a high island massif is present, han on other parts of the same islands (BONNER, 1968 ; SCHULZE, 1971 ; BESTER, 1977).

The coastal topography, and the habitat types available to fur seals on various sub-Antarctic islands is escribed by PAULIAN (1964), BONNER (1968), BUDD (1972), CONDY (1978) and BESTER (in press *a*). Considerable variation exists in the number, and surface area of beaches available to fur seals. This availability argely depends on the length of the coastlines on the different islands, these being, for example, approximately 1 km, 130 km and 3 000 km long at Gough, Marion and the Kerguelen archipelago respectively. Parts of hese coastlines cannot be negotiated by fur seals since the land often terminates abruptly in sea-pounded liffs. As a rule however, the islands used by *A. tropicalis* and *A. gazella* have a number of negotiable beaches n all coasts, with the exceptions of Bouvet, Bird and the McDonald Islands where entire flanks of the islands re bounded by precipitous cliffs. It is generally therefore possible to identify preferences in the local istribution of the fur seals on the various islands.

Beach surface structure and physiognomy vary from sandy, shingle and open boulder beaches and those rewn with angular jumbled rock, to rocky platforms, offshore rocks and islets. Beaches furthermore differ their accessibility to and from the sea, the degree of protection from stormy sea conditions, and access inland vegetated or peaty areas.

INTERACTION

All fur seal populations in the southern ocean show a breeding season peak in their numbers ashore ring the summer (CSORDAS & INGHAM, 1965 ; BONNER, 1968 ; STIRLING, 1971 ; MILLER, 1975 ; CONDY, 1978 ;

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BESTER, 1981). Parous females pup over a short period at this time when optimal physical environmental conditions, notably higher ambient temperatures, for pup survival prevail. This may also be well timed with availability of food resources as an ultimate factor in the fur seal's seasonal haulout cycle, since optimal physical environmental factors and adequate food supply are closely linked (LING, 1969). However, as climatic factors, particularly air temperatures, are a major variable between high and low latitude islands the behavioural response of fur seals to the degree and frequency of exogenous thermal loading may be manifested in their local distribution and habitat selection. Fur seals with land based commitments, that is parturient females that initially remain nursing their newborn pups, and territorial males that establish and maintain territories where the females congregate, would have more cause to avoid thermal overloading. The formation and location of particularly breeding colonies would therefore serve as useful indicators of the impact of the environment on the fur seals at the different islands.

Figure 1 shows the distribution of fur seal breeding colonies at islands over the entire distributional range

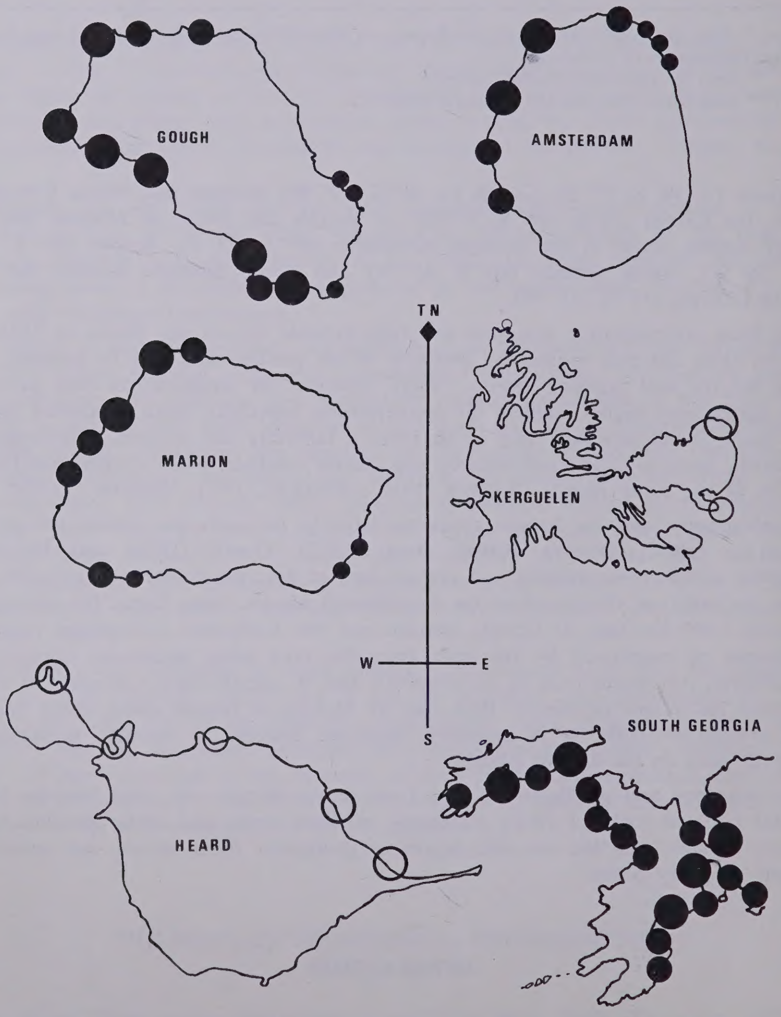

FIG. 1. — Distribution of breeding (•) and nonbreeding (○) colonies of fur seals on sub-antarctic islands. Data were procured from BUDD (1972), TOLLU (1974), PAYNE (1977), CONDY (1978), and BESTER (in press, *a* and *b*).

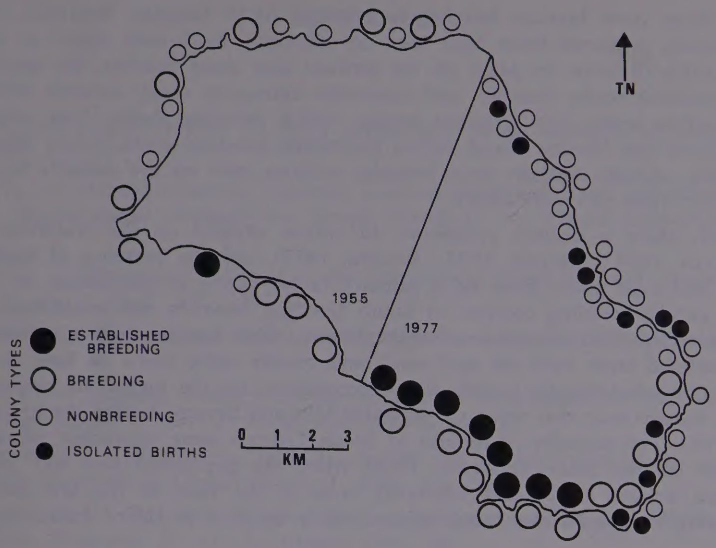

FIG. 2. — Past and present distribution of *A. tropicalis* at Gough Island (after BESTER, *in press a*).

A. tropicalis and *A. gazella*. In the absence of significant breeding colonies, the high concentration areas ionbreeding fur seals are shown for example at Kerguelen, and Heard Island. At low latitudes such as on sterdam Island and Gough Island, breeding colonies of *A. tropicalis* are confined to westerly beaches STER, in press *a* ; TOLLU, 1974). South of the Antarctic Convergence, however, *A. gazella* breeding colonies confined to the east coast of, for example, Bird Island, as were nonbreeders at Heard Island, and the rbet Peninsula of Kerguelen (BESTER, in press *b*) which lie on the Convergence. At Marion Island in r only area of sympatry, breeding by both *A. tropicalis* as on northerly islands, and *A. gazella* in contrast igh latitude islands, occurs on windward westerly beaches (CONDY, 1978). These distribution patterns are sistent with the concept that with wind increasing fur seals' tolerance to heat loading through convective loss (PAULIAN, 1964 ; RAND, 1967), the choice of sprayladen, windward west coasts in low latitudes would lerate the effect of exogenous heat loading (BESTER, in press *a*). This preference for windward coasts not apply to fur seals on islands in high latitudes where it would be of little consequence.

Throughout their range *A. tropicalis* and *A. gazella* populations are increasing, for example, the large rapidly increasing populations centered at Gough and South Georgia respectively (PAYNE, 1977 ; BESTER,) a). At Gough,and at Bird Island off the northwestern tip of the mainland of South Georgia, fur seals ıpy all available beaches. The Bird Island population responded to increases by expanding breeding areas. ding colonies occupied all suitable areas, and nuclei of further colonies became established on the cent mainland (Fig. 1). With further increases, colonies responded with a rise in density, but also by ient colonies being established away from dense breeding colonies, up to 35 km distant from the main entration, but also some 125 km away at the opposite tip of South Georgia (PAYNE, 1977). At Gough ıd the extension of breeding colony beaches also occurred with an increase in population size (BESTER,) a). However, breeding colonies remained almost exclusively confined to westerly beaches in spite of congested conditions that developed. All the breeding colony beaches of 1955-56 became permanently olished ones over 22 years, yet only a few small breeding colonies developed on the proximate south-east coast. isolated births occurred on the remaining parts of the leeward east coast (Fig. 2). In contrast, therefore, . *gazella* at South Georgia, *A. tropicalis* females display a reluctance to exploit leeward east coast beaches, rently a thermoregulatory response in the latter group (BESTER, in press *a*).

BONNER (1968) and WILSON (1974) concluded that rocky habitats are preferred by fur seals (*Arctoalus* species). At Gough Island, *A. tropicalis* have little choice other than the selection of rocky beaches rding to its surface structure. Breeding females utilized almost all habitat types on windward westerly beaches. These vary from open boulder beaches to jumbled rocky beaches, provided that they are easi accessible, and sufficiently protected from high seas, for example, by a wide beach or one where adjace higher ground is available (Bester, in press *a*). On leeward east coast beaches, the small breeding coloni are only found on jumbled rocky beaches and accessible extremely rocky sections (Bester, in press *a* Pregnant females therefore select only irregular terrain which provides shelter from direct solar radiatio Also at Amsterdam Island and Marion Island, before population pressure could dictate expansion of the ran of habitat use, breeding colonies similarly used irregular habitats even on the westerly beaches to which the were confined (Paulian, 1964 ; Condy, 1978).

Breeding fur seals show a distinct preference for areas situated on the waterline especially on lo latitude islands (Paulian, 1964 ; Miller, 1974 ; Bester, 1977), and the presence of easily accessible wate for example the sea and tidal pools, may be a primary factor active in the choice of a breeding locatio (Stirling, 1971). *A. gazella* breeding colonies at South Georgia, however, are established chiefly on beach that are sufficiently protected from adverse weather conditions. Adult females show a preference for dry shing beaches, relatively sheltered from both sea and wind, and readily settle down on bare rock (Bonner, 1968 Here, and on other cold sub-Antarctic islands where dependence on the immediate oceanic effect is minim for thermoregulation, harems may also occur on vegetated hills and terraces behind the beaches (Bonner, 1958 Budd & Downes, 1969). The majority of harems at South Georgia were, moreover, situated on the beach that afforded the best landing places (Bonner, 1958) when the population was still low. Non-breeders Kerguelen congregated on the slopes and vegetated areas at the base of the low eastern cliffs (Beste in press *b*) and breeding *A. gazella* even used leeward sandy beaches at Heard Island and McDonald Islan (Budd, 1972).

It can therefore be concluded that the local distribution and habitat selection of fur seals at low latitu islands are primarily a behavioural adaptation resulting from high ambient temperatures. In high latitud the emphasis shifts to protection from the onslaught of westerly storms. It appears unlikely that biotic factor for example competition for space with the southern elephant seal *Mirounga leonina,* and the effect of huma exploitation, have had a significant influence in this respect. It can be argued that a remnant fur seal populatio subjected to indiscriminate sealing operations in the past, would spread from inaccessible parts of an islan Bester (in press *a*), however, concluded that the present local distributions of fur seal populations cann be ascribed to a defense reaction to exploitation (after Paulian, 1964), such exploitation making itself fe only initially at the most. Although large *M. leonina* populations occur on especially the high latitude island their distribution overlaps with those of fur seals at easily accessible leeward east coast beaches. There i however, a spatial separation between the two groups as elephant seals prefer broad open beaches of san or shingle (Bonner, 1968). Moreover, at Amsterdam Island and Gough Island (Paulian, 1964 ; Bester, 1980 very few elephant seals occur, although the fur seals show a highly specific distribution pattern. On all th islands of sympatry, the breeding seasons of the fur and elephant seals are temporally separated and therefo no real need to compete for breeding colony beaches arises. This conforms to Ling's (1969) hypothesis th in the adjusted annual cycles and different habitat requirements lies the successful co-existence between speci which compete for space on land.

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